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Does torpor of elephant shrews differ from that of other heterothermic mammals?

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Torpor bouts of elephant shrews are intermediate in duration to those of daily heterotherms and hibernating mammals, but their body temperatures (T_b s) and metabolic rates are very low and similar to those of hibernating mammals. We quantified the thermal physiology of the Cape rock elephant shrew (*Elephantulus edwardii*), a species endemic to high-altitude regions of South Africa, where winters are cold and wet, and tested whether it displays multiday torpor characteristic of hibernators at low ambient temperature (T_a). *E. edwardii* regularly displayed torpor over a wide range of T_a s. Occurrence of torpor and duration of torpor bouts increased with decreasing T_a . Whereas normothermic T_b was stable, T_b in torpid individuals fell with T_a . The mean $T_b - T_a$ differential at the minimum T_b was 0.7°C, and the mean minimum T_b at T_a 8.9°C was 9.3°C. Duration of torpor bouts ranged from 6.5 to 44 h and was correlated negatively with T_a and T_b during torpor. Time required for the reduction of T_b to a $T_b - T_a$ differential of <2.0°C was faster for >1-day torpor bouts than those lasting ≤1 day, suggesting that the duration of a bout might be determined at the beginning, not during, a bout. The nature of heterothermy in *E. edwardii* seems qualitatively similar to that of other elephant shrews, although torpor is somewhat deeper and longer in this species. Temporal patterns of torpor in *E. edwardii* differ from those of most cold-climate hibernators, likely for ecological rather than physiological reasons.

Key words: body temperature, cooling and rewarming rates, Macroscelidea, torpor occurrence and duration

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Torpor is used by diverse mammals belonging to >50% of all mammalian orders. Because torpor is characterized by pronounced reductions in body temperature (T_b) and metabolic rate, it is the most effective strategy for energy conservation available to mammals (Boyer and Barnes 1999; Geiser 2004; Merritt 2010). In contrast to homeothermic mammals, which are incapable of using torpor, species using torpor are often referred to as heterotherms, and most of these appear to belong to 2 distinct groups, the hibernators—species capable of employing prolonged, multiday torpor—and the daily heterotherms—species capable of daily torpor usually lasting only part of a day (Geiser and Ruf 1995).

Hibernation in many species consists of a sequence of multiday torpor bouts (often 1–3 weeks) interrupted by periodic rewarming and brief (hours) normothermic periods when high T_b s are maintained. Hibernation often is seasonal, usually lasts from late summer–autumn to late winter–spring, and occurs especially, but not exclusively, at low ambient temperature (T_a). The duration of torpor bouts generally increases with decreasing T_a over a wide range of T_a s, and

although torpor bouts can last for weeks at low T_a , at high T_a they can last only for hours and superficially might appear to be daily torpor (Geiser and Brigham 2000; Song et al. 1997). Torpid hibernators have extremely low T_b (often between 0°C and 10°C), metabolic rates, and $T_b - T_a$ differentials, which might explain why they are capable of multiday torpor bouts and does explain why they can survive for months on stored body fat (Bieber and Ruf 2009; Boyer and Barnes 1999; Song et al. 1997).

Daily heterotherms, in contrast to hibernators, are incapable of multiday torpor bouts. Daily torpor lasts only for hours and usually, but not always (Körtner and Geiser 2009), requires daily foraging and feeding (Geiser and Ruf 1995; McKechnie and Lovegrove 2002). Because during daily torpor T_b , metabolism, and the $T_b - T_a$ differentials generally are substantially higher than in hibernators, daily heterotherms



have relatively higher energy requirements during torpor and apparently require regular uptake of food to maintain a balanced energy budget.

Whereas most variables in relation to torpor examined statistically show a strong bimodal distribution and place heterothermic mammals into 1 of these 2 groups, a few species apparently do not fit these general patterns. For example, some species of elephant shrews (Macroscelidea) show low T_b and metabolic rates similar to those of torpid hibernators (Lovegrove et al. 2001). However, their torpor bouts tend to be short and usually last for 8–10 h, with a maximum of 20.3 h in the laboratory and 39 h in the field (Lovegrove et al. 2001; Mzilikazi and Lovegrove 2004, 2005; Mzilikazi et al. 2002). Nevertheless, quantitative data on duration of torpor bouts as a function of T_a in elephant shrews are currently limited, and torpor has not been examined under conditions that often are used to examine hibernation; that is, at $T_a < 10^\circ\text{C}$ when food is withheld.

The purpose of our study was to investigate whether torpor is expressed in the Cape rock elephant shrew (*Elephantulus edwardii*), which is endemic to South Africa. The species is restricted to relatively high altitudes but has not been shown to undergo torpor (Leon et al. 1983). If *E. edwardii* proved to be heterothermic, we were interested in quantifying how duration of torpor bouts is related to T_a . The duration of torpor bouts is affected strongly by T_a in other species (French 1985; Geiser and Kenagy 1988), and exposure to low T_a should reveal whether the species is capable of multiday torpor. *E. edwardii* seems to be particularly interesting in this regard because it lives in an area that experiences semiarid conditions for about half the year and especially during hot summers, whereas in winter it is exposed to cold and wet and occasionally snow. Because *E. edwardii* lives in a winter rainfall area, it is unlikely that it regularly uses exogenous heat uptake (basking) in winter, as does, for example, *E. myurus* from a summer rainfall area in which torpor bouts seem to be terminated by basking in the sun (Mzilikazi et al. 2002).

MATERIALS AND METHODS

Rock elephant shrews (*E. edwardii*; 4 females and 3 males), were trapped at an altitude of approximately 700 m at Gamkaberg Nature Reserve (33°38'S, 21°59'E) near Oudtshoorn, South Africa, a winter rainfall area with mean annual precipitation of approximately 400 mm. The prevailing photoperiod in midwinter (July) is close to 10L:14D (sunrise at 0730 h and sunset at 1745 h), and the average minimum and maximum T_a are 9°C and 21°C , respectively (Gamkaberg Nature Reserve records). Animals were captured from 4 to 10 June 2008 (austral winter) in Sherman box traps (H. B. Sherman Traps, Inc., Tallahassee, Florida) baited with peanut butter and rolled oats and checked in the early morning after 1 night of trapping. Animals were transferred to the Zoology Department, Nelson Mandela Metropolitan University, Port Elizabeth, where they were held individually in large terraria provided with wood shavings and nest boxes in a constant

temperature room at $T_a 20^\circ\text{C}$. Initially, animals were fed daily ad libitum, alternating between a mixture of ProNutro (Bokomo, South Africa) soaked in water (18% ProNutro powder, consisting of 22% protein, 59% carbohydrate, and 6% fat, soaked in 82% water) or canned dog food; water was provided ad libitum. To provide a continuous record of T_b temperature data loggers (iButtons DS 1922L, resolution 0.06°C ; Maxim, Sunnyvale, California) were calibrated to the nearest 0.1°C , programmed to read T_b every 30 min, waxed (mass 3.3 g including wax), sterilized, and implanted intraperitoneally under sterile conditions. Oxygen–isoflurane was used for anesthesia. After surgery on 13 June animals were kept in a precisely controlled constant temperature room at $T_a 24.8^\circ\text{C} \pm 0.1^\circ\text{C}$ for recovery for 4 days, which continued at 18.4°C because this T_a represents only a mild cold load. To mimic autumnal cooling T_a was reduced stepwise: on 17 June to $T_a 18.4^\circ\text{C} \pm 0.1^\circ\text{C}$, on 24 June to $15.4^\circ\text{C} \pm 0.1^\circ\text{C}$, on 1 July to $12.2^\circ\text{C} \pm 0.1^\circ\text{C}$, on 8 July to $8.9^\circ\text{C} \pm 0.1^\circ\text{C}$, and on 29 July to $18.4^\circ\text{C} \pm 0.1^\circ\text{C}$ for the remainder of the measurements. We quantified T_b as a function of T_a in this experiment because our main aim was to determine whether the species can express multiday torpor, and this approach required only limited disturbance and handling. Metabolic measurements would have required frequent disturbance or handling, or both, which would have interfered with our aim and was unnecessary because it is well established that T_b and metabolic rate in thermo-conforming torpid mammals are closely correlated (Geiser 2004; Song et al. 1997). T_a was recorded in the constant temperature room with an iButton (DS 1922L) at 30-min intervals. Most animals ($n = 6$) thrived in captivity, but 1 female, the lightest individual at capture, died after 2 weeks in captivity.

Food was provided ad libitum daily until 9 July ($T_a 8.9^\circ\text{C}$); from that date animals were fed every 2nd day to ensure torpid individuals were not disturbed daily and aroused prematurely from a torpor bout. At the end of measurements iButtons were removed under general anesthesia, as described above. Because 2 of the iButtons failed, data are reported for 4 individuals (2 females and 2 males).

Animals were considered torpid when their T_b fell below 30°C (see “Results”), and duration of torpor bouts was calculated from the time T_b remained below 30°C . Times of entries and arousals from torpor were examined by a Rayleigh test (Z; Zar 1999) to determine whether times differed significantly from a random distribution. Maximum entry and arousal rates were calculated for the 30 min for which the most pronounced change of T_b was measured. To examine whether physiological variables are interrelated or related to T_a , linear regressions, fitted by the method of least squares, were used; residuals were examined for homoscedasticity. To test for differences between mean values of variables t -tests were used; the Kolmogorov–Smirnov test was used to test for normality. Statistical analyses were accomplished using StatistiXL (version 1.8; statistiXL, Nedlands, Western Australia, Australia). Numeric values are given as means ± 1 SD.

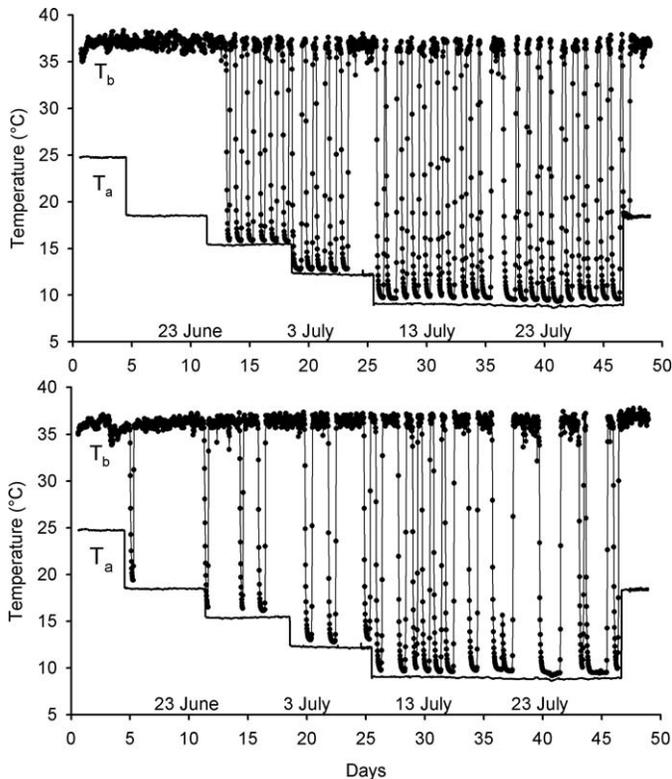


FIG. 1.—Body temperature (T_b) fluctuations of 2 *Elephantulus edwardii* (top, male; bottom, female) exposed to different ambient temperatures (T_a) as a function of time. Each point represents an individual reading of T_b .

Permits for animal experimentation were provided by the Animal Ethics Committee of the University of New England, the Nelson Mandela Metropolitan University, and the Cape Nature Conservation Board. Experimentation followed the guidelines of the American Society of Mammalogists (Gannon et al. 2007).

RESULTS

Body mass of the 4 elephant shrews was 47.5 ± 4.7 g before surgery when animals were fed ad libitum. One week after surgery body mass (without iButtons) had declined to 41.9 ± 4.2 g; however, body mass over the next 2 weeks increased again to 45.4 ± 2.9 g. When food was provided only every 2nd day at T_a 8.9°C , body mass again declined to 41.8 ± 1.9 g.

Elephant shrews frequently displayed torpor in the laboratory at T_a s of $<24.8^\circ\text{C}$ (Fig. 1). Torpor was observed occasionally at T_a 18.4°C , even though food was freely available, but torpor use increased with decreasing T_a . Although at T_a 18.4°C and 15.4°C only 2 or 3 individuals used torpor, at T_a 12.2°C and 8.9°C all 4 individuals expressed torpor. Occurrence of torpor (days torpid/days measured) was 32% at T_a 15.4°C , 39% at 12.2°C , and 95% at 8.9°C . At T_a 8.9°C , when food was withheld on every 2nd day, no difference in torpor use was observed between days with and without food because torpor occurred on almost all days. Torpor occurrence also did not appear to differ between sexes;

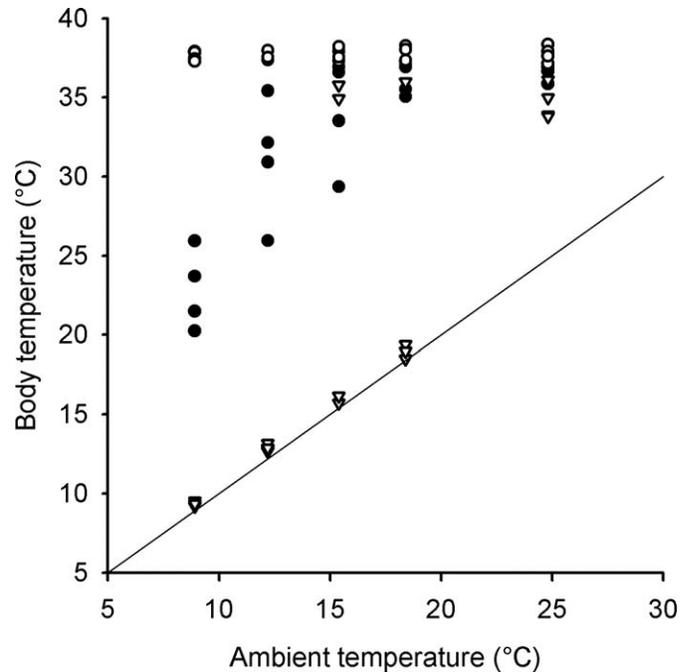


FIG. 2.—Body temperature (T_b) as a function of ambient temperature (T_a) in 4 *Elephantulus edwardii*. Maximum T_b (circles), mean T_b (dots), and minimum T_b (triangles) are shown. Each point represents the mean for an individual, and the diagonal line represents $T_b = T_a$.

females displayed a total of 15.5 ± 4.9 bouts, males 20.5 ± 16.3 bouts.

Torpor patterns were affected strongly by T_a (Fig. 1). Torpor bouts lasting for <24 h were observed at all T_a s $<24.8^\circ\text{C}$, but those lasting >24 h were observed only at T_a 8.9°C , the lowest T_a measured.

The maximum T_b during the active phase was not affected by T_a ($r^2 = 0.01$, $F_{1,18} = 0.18$, $P = 0.676$) and was $37.7^\circ\text{C} \pm 0.5^\circ\text{C}$ at T_a 24.8°C and $37.6^\circ\text{C} \pm 0.3^\circ\text{C}$ ($n = 4$) at T_a 8.9°C (Fig. 2). However, mean T_b declined significantly ($y = 19.5 + 0.793x$, $r^2 = 0.61$, $F_{1,18} = 27.70$, $P < 0.0001$) from $36.6^\circ\text{C} \pm 0.5^\circ\text{C}$ at T_a 24.8°C to $22.8^\circ\text{C} \pm 2.5^\circ\text{C}$ at T_a 8.9°C . The minimum T_b of torpid individuals also changed with T_a ($y = -4.28 + 1.60x$, $r^2 = 0.67$, $F_{1,18} = 36.16$, $P < 0.0001$) and fell close to T_a over the entire T_a range torpor was observed (Figs. 1 and 2). The mean minimum T_b at T_a 8.9°C was $9.3^\circ\text{C} \pm 0.1^\circ\text{C}$ ($n = 4$), and the individual minimum T_b was 9.2°C . The $T_b - T_a$ differential when T_b was minimal ranged between 0.2°C and 1.2°C , and the mean was $0.7^\circ\text{C} \pm 0.2^\circ\text{C}$. Over the T_a range from 18.4°C to 12.2°C the $T_b - T_a$ differential was not affected by T_a ($r^2 = 0.03$, $F_{1,21} = 0.64$, $P = 0.434$). However, when $T_b - T_a$ differentials at T_a 8.9°C were included in the linear regression, a weak but significant relationship was observed ($T_b - T_a$ [$^\circ\text{C}$] = $1.03 - 0.029T_a$ [$^\circ\text{C}$]; $r^2 = 0.13$, $F_{1,70} = 10.74$, $P = 0.002$), suggesting that at the lowest T_a measured the $T_b - T_a$ differential was raised somewhat, perhaps from thermoregulation. Similarly, the relationship between duration of torpor bout and the $T_b - T_a$ differential was not significant ($r^2 = 0.04$, $F_{1,70} = 2.63$, P

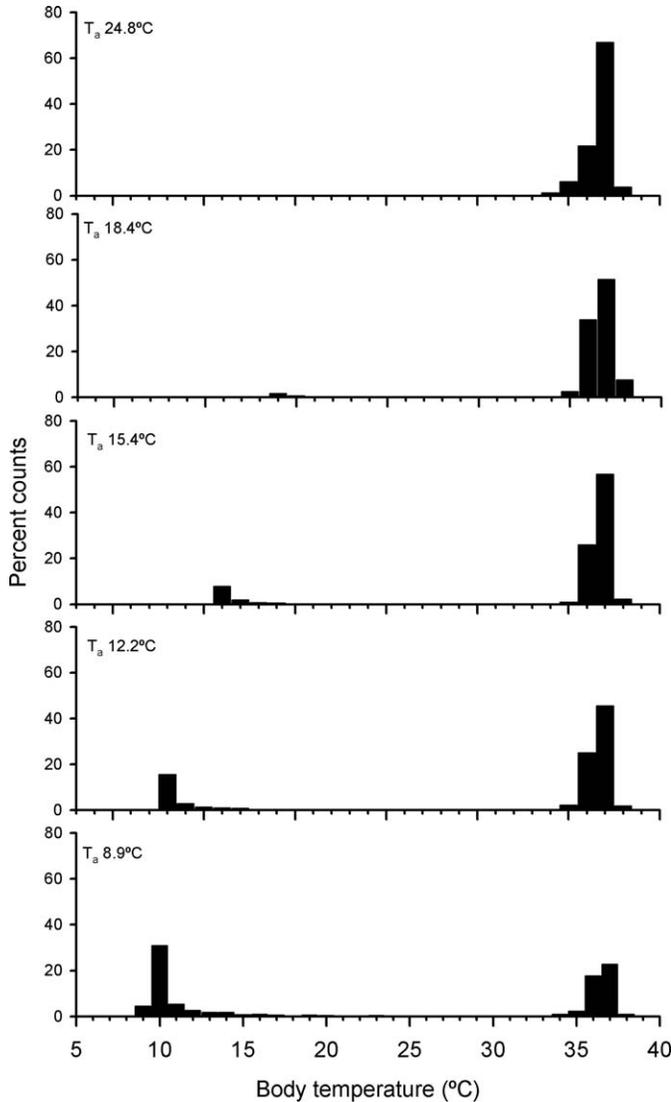


FIG. 3.—Frequency distribution of percent body temperature (T_b) integers of 4 *Elephantulus edwardii* at the 5 ambient temperatures (T_a) measured.

= 0.11) when all bouts over the entire T_a range where torpor was observed were regressed. However, when only bouts of <20 h duration were regressed, the $T_b - T_a$ differential was correlated negatively with torpor bout duration ($T_b - T_a$ [°C] = $1.37 - 0.39$ bout duration [h]; $r^2 = 0.35$, $F_{1,39} = 22.50$, $P < 0.001$). This regression intersected the mean $T_b - T_a$ differential of 0.7°C at 17 h, suggesting that this bout duration is required for the species to reach its steady-state minimum T_b .

Although the mean maximum T_b was not affected significantly by T_a , the frequency distribution of integers of normothermic T_b changed with T_a (Fig. 3). Whereas T_b 36°C and 37°C encompassed 21.7% and 67% of all T_b s measured at T_a 24.8°C , these proportions changed and declined with decreasing T_a , and at T_a 8.9°C T_b 36°C and 37°C made up only 17.7% and 22.8% of all T_b s, respectively. In contrast, the proportion of T_b s below 20°C increased with decreasing T_a ,

and at T_a 8.9°C T_b 10°C represented the largest proportion (31%) of all T_b s measured. T_b s between 33°C and 20°C were represented by <0.6% of all T_b s measured at the T_a s where torpor was observed. T_b 30°C was represented on average over all T_a s by only 0.13% of T_b s measured; therefore it was the most transient of T_b s measured between normothermia and torpor and consequently seems most suitable as the threshold T_b for defining torpor in this species. Nevertheless, the other T_b s—for example, $31\text{--}33^\circ\text{C}$ —frequently used for defining T_b thresholds for torpor (Barclay et al. 2001; Willis and Brigham 2003) also were rarely observed (0.15–0.2% of all T_b s). Thus, any of these T_b s ($30\text{--}33^\circ\text{C}$) could be used safely for defining torpor without having any significant effect on other derived variables relying on a threshold T_b .

Torpor bouts lasted between 6.5 and 44 h, and the mean bout duration was 17.3 ± 8.3 h. Overall, 9 of the total 72 torpor bouts observed lasted for >1 day and were observed in 3 individuals (1 female and 2 males); the mean duration of these bouts was 35.6 ± 8.4 h. The mean maximum duration of torpor bout for the 4 individuals was 32.4 ± 12.5 h. Of the >1-day torpor bouts, those bouts that lasted for >40 h (5 bouts in 1 female and 1 male) began on days no food was provided, but arousals also occurred on days when no food was provided. For >1-day bouts lasting <30 h (4 bouts in 2 males) entry into torpor occurred on days food was provided, but all animals also aroused on days they were not fed, suggesting that all arousals from >1-day bouts were not caused by disturbance.

Torpor bout duration at T_a 18.4°C and 15.4°C did not differ significantly ($t_{10} = 0.51$; $P > 0.66$); however, the duration of all torpor bouts was correlated negatively ($r^2 = 0.15$, $F_{1,67} = 11.81$, $P = 0.001$) with T_a between 15.4°C and 8.9°C . Torpor bout duration (\log_{10}) was strongly correlated with the minimum T_b over the entire range of T_a s measured ($r^2 = 0.27$, $F_{1,70} = 14.87$, $P < 0.0001$; Fig. 4). At each separate T_a torpor bout duration and minimum T_b were correlated only at T_a 8.9°C ($r^2 = 0.17$, $F_{1,47} = 9.49$, $P = 0.003$) and T_a 12.2°C ($r^2 = 0.41$, $F_{1,9} = 6.23$, $P = 0.034$), but not correlated (T_a 15.4°C : $r^2 = 0.28$, $F_{1,7} = 2.77$, $P = 0.14$; T_a 18.4°C : $r^2 = 0.80$, $F_{1,1} = 4.05$, $P = 0.29$) at the other T_a s, likely because of the limited data. However, mean T_b during a torpor bout and duration of torpor bout at each of the 3 low T_a s examined showed strong negative linear relationships ($r^2 \geq 0.57$, $P < 0.01$) when plotted on logarithmic scales (Fig. 5).

Both torpor entries and arousals were nonrandom and occurred at specific times of day (entries: $Z = 32.78$, $P < 0.001$; arousals: $Z = 52.77$, $P < 0.001$; Fig. 6). Entry into torpor occurred at a mean angle of $279.1^\circ \pm 50.8^\circ$ or 1836 \pm 0323 h (Rayleigh test), whereas arousals occurred at a mean angle of $161.1^\circ \pm 31.9^\circ$ or 1044 \pm 0207 h. Although the mean time of torpor entry at T_a 8.9°C between torpor bouts lasting <1 day (entry time 1840 \pm 0312 h) and torpor bouts lasting >1 day (entry time 1530 \pm 0249 h) was indistinguishable (95% confidence intervals [95% CIs] overlapped), in the 3 individuals that employed >1-day bouts the time of arousal differed significantly by about 3 h (<1 day: 1029 \pm 0135 h;

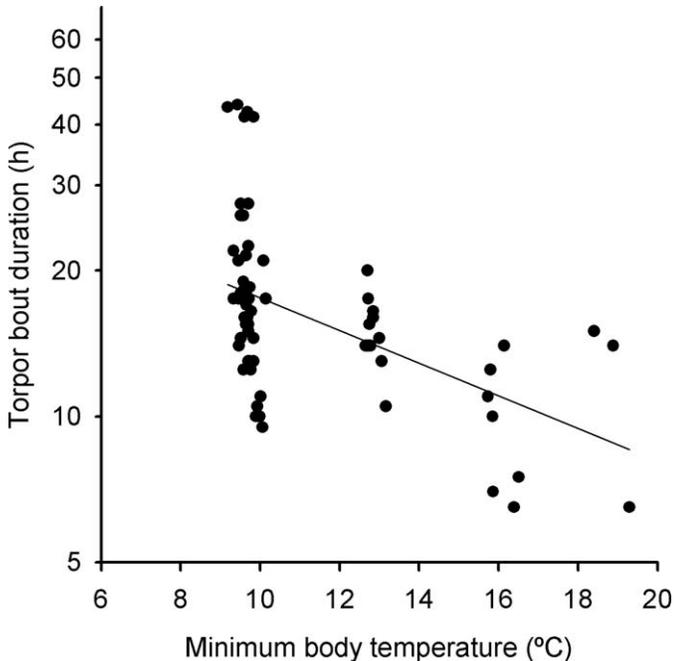


FIG. 4.—The duration of torpor bouts as a function of the minimum body temperature (T_b) during a torpor bout in 4 *Elephantulus edwardii*. The regression equation was: $\log_{10}y = 1.58 - 0.00337x$; $r^2 = 0.27$, $F_{1,70} = 14.87$, $P < 0.0001$.

>1 day: 1324 ± 0143 h; no overlap and 14.4° or almost 1-h gap in 95% CI).

Maximum cooling rates during entry into torpor differed (T_a 15.4°C : $t_4 = 3.02$, $P = 0.039$; T_a 12.2°C : $t_6 = 8.25$, $P < 0.0001$; T_a 8.9°C : $t_6 = 6.54$, $P = 0.001$) from maximum rewarming rates at all T_a s, with the exception of T_a 18.4°C , where only limited data were available. Moreover, the overall individual means for maximum torpor entry rates at all T_a s ($0.26 \pm 0.015^\circ\text{C}/\text{min}$) differed ($t_6 = 5.14$, $P < 0.01$) from the overall maximum rewarming rates ($0.38 \pm 0.035^\circ\text{C}/\text{min}$). Further, the time required to reduce the $T_b - T_a$ differential to $<2.0^\circ\text{C}$ was significantly ($t_4 = 2.65$, $P < 0.05$) less for >1-day than <1-day bouts by 38 ± 4 min in the 2 individuals that displayed multiple >1-day torpor bouts.

DISCUSSION

Our study shows that *E. edwardii*, although described as homeothermic in a previous study (Leon et al. 1983), regularly displays torpor in the laboratory both when food is available and when it is restricted. Torpor bouts lasted for up to almost 2 days, which is longer than those reported in other elephant shrews. However, multiday torpor bouts lasting for up to several weeks as characteristic of many hibernators were not observed here, although the metabolic rates during torpor had to be extremely low to allow a T_b to approach within 0.7°C of T_a in ~ 45 -g *E. edwardii*.

As in many other heterothermic species, occurrence of torpor in *E. edwardii* increased with decreasing T_a . At T_a 8.9°C occurrence of torpor was 95%, similar to many

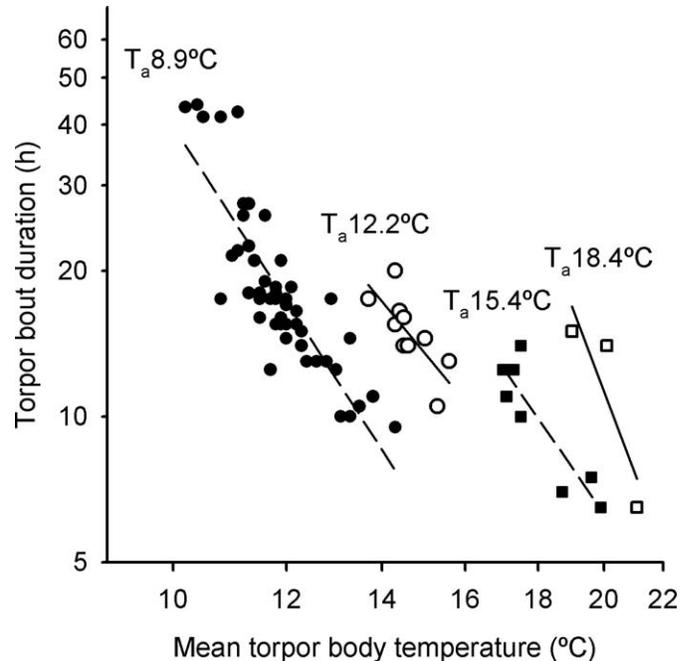


FIG. 5.—Duration of torpor bouts as a function of the mean body temperature (T_b) during a torpor bout at different ambient temperatures (T_a) of 4 *Elephantulus edwardii*. The regression equations were:

$$T_a \ 8.9^\circ\text{C} : \log_{10}y = 6.17 - 4.57 \log_{10}x; \ r^2 = 0.74, \ F_{1,47} = 133.20, \ P < 0.0001;$$

$$T_a \ 12.2^\circ\text{C} : \log_{10}y = 5.34 - 3.58 \log_{10}x; \ r^2 = 0.57, \ F_{1,9} = 11.77, \ P < 0.01;$$

$$T_a \ 15.4^\circ\text{C} : \log_{10}y = 6.35 - 4.27 \log_{10}x; \ r^2 = 0.81, \ F_{1,7} = 30.91, \ P < 0.002;$$

and

$$T_a \ 18.4^\circ\text{C} : \log_{10}y = 11.2 - 7.8 \log_{10}x; \ r^2 = 0.28, \ F_{1,1} = 3.49, \ P = 0.28.$$

hibernators and daily heterotherms in which occurrence of torpor at low T_a often approximates 100%, especially in the wild (Körtner et al. 2010; Stawski et al. 2009). Nevertheless, unlike in many hibernators, the torpor season in *E. edwardii* is not composed of a sequence of long torpor bouts interrupted by regular brief normothermic periods, but rather by frequent long or short torpor bouts that are interspersed by normothermic periods lasting from a few hours to >1 day (Fig. 1), likely in part for foraging. This pattern of torpor interspersed by activity seems appropriate for a species that lives in a region where it can forage and feed for prolonged periods (in contrast to, for example, one living in snow-covered alpine regions) and that relies on a diversity of invertebrates including ants and termites, some of which will be available all year (Lovegrove et al. 1999). Moreover, like other species of elephant shrews but unlike many hibernating species (Kenagy and Barnes 1988), *E. edwardii* does not show substantial

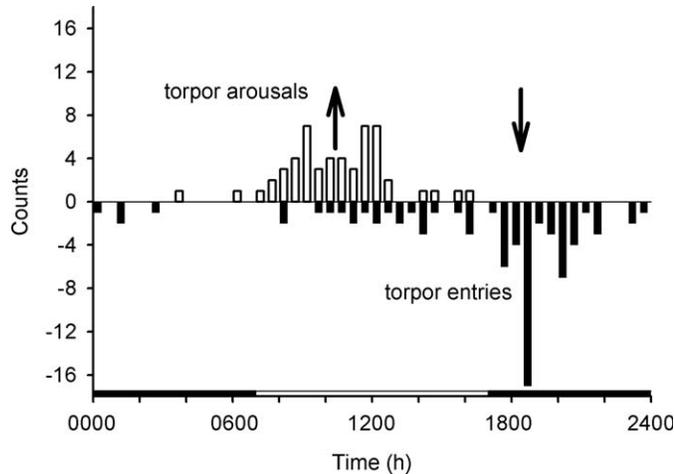


FIG. 6.—Timing of torpor entries (bottom) and arousals (top) in 4 *Elephantulus edwardii*. Arrows indicate average entry (\downarrow) and arousal (\uparrow) times as determined by Rayleigh tests. The bars at the bottom of the figure indicate the scotophase (dark) and photophase (light).

autumnal fattening (Mzilikazi et al. 2002). The absence of autumnal fattening should not limit multiday torpor bouts physiologically (Stawski et al. 2009), but an animal should forage regularly to ensure that limited body energy reserves are not depleted entirely.

The duration of torpor bouts of *E. edwardii* (overall mean 17.3 h, mean maximum 32.4 h, longest bout 44 h) was long for daily heterotherms measured in the laboratory (mean maximum bout duration 11.2 h) but short for hibernators (mean maximum 355 h, minimum 96 h—Geiser and Ruf 1995). The mean duration of torpor bouts of *E. edwardii* fell within the range of maximum torpor bouts in daily heterotherms, but the maximum bout duration (44 h) was 4-fold that of the mean maximum for daily heterotherms and about one-half as long as that of the shortest maximum bout (96 h) observed in hibernating species. Why does *E. edwardii*, despite its low T_b and $T_b - T_a$ differential, not display longer torpor bouts? In several species torpor bouts are substantially longer in the field than in the laboratory (Körtner and Geiser 2009). Although this also might be possible in *E. edwardii*, it is likely that, even in the wild and in agreement with field data on other elephant shrews (Mzilikazi et al. 2002), it does not display the classic hibernation pattern of multiday bouts interspersed by brief normothermic periods for reasons related to climate, food, and fattening, as outlined above. Moreover, it is unlikely that *E. edwardii* experiences a prolonged hibernation season without foraging because we were able to trap it in winter.

Periodic rewarming from torpor has been observed in all heterothermic mammals studied to date, and although rewarming is usually energetically very costly and the reasons for its regular repetition are frequently discussed, currently no mechanism to explain its occurrence is widely recognized. Proposed explanations often infer some function that cannot

be accomplished at low T_b during torpor and requires a high T_b to be achieved (Körtner and Geiser 2000; Nemeth et al. 2010; Prendergast et al. 2002). Because, in many species duration of torpor bouts increases with decreasing T_a , T_b , and metabolism over a wide range of T_a s (i.e., the T_a range in which torpid individuals are thermo-conforming), it is often assumed that torpor bout length is related to some metabolic process that is dependent on temperature (French 1985; Geiser and Kenagy 1988).

In our study the duration of torpor bouts was correlated with T_a , the minimum T_b during torpor, the mean T_b during torpor, and for bouts of <20 h the $T_b - T_a$ differential, supporting these interpretations to some extent. However, because low T_b is used for defining torpor and the $T_b - T_a$ differential is at least partially a function of torpor bout duration—that is, it takes time for the body to cool—some of these apparent correlations can be based on circular reasoning. It is not surprising that the average T_b , for example, is related to torpor bout duration because the longer an animal is in torpor the lower its average T_b (and also average torpor metabolic rate) should be. However, this does not necessarily mean these variables are functionally linked. Although maximum cooling rate of *E. edwardii* did not differ, one of the significant differences between torpor bouts of <1 day and those of >1 day was that the time to reach a $T_b - T_a$ differential of $<2.0^\circ\text{C}$ was significantly shorter in the latter. Although this observation is based on limited data and requires verification from other species, the difference does suggest that the decision to enter a short or long torpor bout was determined at the time of entry into torpor because elephant shrews reduced T_b to near T_a faster before long bouts than before short ones. This interpretation also is supported by the observation that of the >1 -day bouts, >40 -h bouts began on days no food was provided, whereas <30 -h bouts all began on days food was provided. This suggests that nutritional status at the beginning of a bout might be linked to its subsequent duration. This new observation in *E. edwardii* differs from previous hypotheses on determination of torpor bout duration because it suggests that the time an animal remains in torpor might be determined before or at entry into torpor, not during the event, as is usually assumed. This is especially interesting because the timing of torpor entry did not differ between short and long bouts, whereas the time of arousal did (i.e., a 3-h delay occurred on >1 -day bouts).

Our study provides further evidence that many presumed homeothermic mammals are heterothermic. It emphasizes that superficial and short-term examination of thermoregulatory patterns does not necessarily reveal whether a species is able to use torpor. This is important because misclassification will result in wrong predictions about the biology and especially energy and foraging requirements of mammals in the wild. Our study adds another species to an increasing number of heterothermic mammals. Although in the past a widely held view was that torpor is rare and occurs only in a few cold-climate species, recent work has shown that torpor is employed widely in all climate zones (Dausmann 2008;

Körtner et al. 2010); for example, in Australia, some 43% of all terrestrial mammals are likely to be heterothermic (Geiser and Körtner 2010). Employment of torpor has enormous implications for increasing short-term survival because low energy and foraging requirements reduce exposure to predators (Stawski and Geiser 2010). Moreover, torpor is also important for long-term persistence of mammals that are exposed to anthropogenic destruction of habitat and introduction of competitors or predators (Geiser and Turbill 2009; Liow et al. 2009) and might help explain why *E. edwardii* is not threatened by extinction.

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